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Evolution of Pseudo-Arrhenotoky

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ABSTRACT

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In arrhenotokous arthropods, males arise from unfertilized eggs. Hence, by controlling the fertilization process mothers can adjust the sex ratio in their offspring. In pseudo-arrhenotokous phytoseiid mites, however, males are haploid, but arise from fertilized eggs. The haploid state is achieved through elimination of the paternal chromosome set during embryonic development. It is shown in this paper that phytoseiid females can control the sex ratio in their offspring and that this control seems as flexible as in arrhenotokous arthropods. As predicted by current evolutionary theory of sex allocation, sex ratios approached half males/half females under random mating, whereas a female bias was observed under sib-mating. The importance of these results for understanding the adaptive significance of pseudo-arrhenotoky is discussed. It is suggested that arrhenotoky is selected for when there is a substantial risk to the females of remaining unmated. When this risk of becoming a 'wall-flower' is low, pseudo-arrhenotoky may evolve because it retains the possibility to reinstal lost genetic information in the maternally derived chromosome by using the paternal chromosome as a template for DNA-repair. The retention of the diploid state in males during embryonic development may thus have certain advantages. It is argued that pseudo-arrhenotoky may be an adaptive genetic system under certain conditions, and not an unstable system that readily reverts to diploidy or evolves towards arrhenotoky or thelytoky.

INTRODUCTION

In an outstanding book on the evolution of sex-determining mechanisms, Bull (1983) devoted several chapters to the selective advantages of producing uniparental males. Despite many variations in uniparental male systems, each shares the property that males are effectively haploid and transmit the maternal genome only. Such systems include arrhenotoky where males arise from unfertilized eggs, and pseudo-arrhenotoky where males arise from fertilized

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eggs but become haploids after inactivation (heterochromatization) and/or elimination of the paternal chromosome set. Exactly when the loss of the paternal chromosomes occurs depends on the organism under study. In some scale insects, somatic tissues retain the paternal chromosome in an active state, whereas it is eliminated in the germ line just before or during spermatogenesis. In phytoseiid mites, chromosome loss or inactivation occurs early in embryogenesis but not until after some mitotic divisions have taken place (Nelson-Rees et al., 1980). As far as we know now, pseudo-arrhenotoky is a relatively rare phenomenon compared to arrhenotoky. However, it has evolved independently at least three times in the arthropods and, because it is much less easy to detect than arrhenotoky and because it has not been investigated systematically, it might be much more widespread than is currently thought.

According to Bull (1979, 1983) the selective advantage for the evolution of male haploidy stems from a two-fold representation of maternal genes in gametes of haploid sons in comparison to diploid sons of biparental origin. The probability of gene identity-by-descent between grandmother and grandchild through uniparental sons is therefore double the probability through biparental sons. This two-fold advantage of producing uniparental sons may overcome the potential lower fitness of these sons and may therefore be the key to our understanding of the advantage of male haploidy. As noted by Bull (1979, 1983) the two-fold advantage provides a selective basis not only for male haploidy but also for the evolution of any genetic system in which the genes of one parent are excluded from gametes in the offspring of one sex. Bull (1979, 1983) therefore considered four different systems with two sexes in which offspring of one sex transmit only the genome inherited from one parent. His preliminary conclusion was that systems with males transmitting only the maternal genome are more stable compared to the other three systems, which lack recombination (and may thus go extinct) and/or which are more likely to revert to diploidy or to evolve towards thelytoky. Bull (1979) also provided an argument why pseudo-arrhenotoky may be more rare than arrhenotoky. Because uniparental males increase the transmission of maternal genes at the expense of the would-be father, there is selection in the most extreme form of genes that when transmitted through sperm avoid this elimination. Under arrhenotoky, sperm do not enter the eggs destined to become males; hence, there is no opportunity for paternal gene expression in sons. However, under pseudo-arrhenotoky sperm penetrates all eggs, and any paternal mutant that avoids loss once in the egg of a son is favoured. Thus, there is this extra factor that may render pseudo-arrhenotoky somewhat more susceptible than arrhenotoky to revert to diploidy. This argument may especially hold soon after the origin of pseudo-arrhenotoky but it is not a very satisfactory answer, because it is equally valid to argue that, under arrhenotoky, there will be selection on paternal genes coding for any ploy to circumvent the mechanisms by which mothers prevent eggs from becoming fertilized. It is therefore of interest to find more decisive factors forcing evolutionary pathways to either arrhenotoky or pseudo-arrhenotoky.

Another advantage of arrhenotoky is that it allows the mother to control the sex of her offspring by influencing the fertilization of each egg. In this way, arrhenotoky provides a flexible mechanism to change the sex ratio of the offspring in an adaptive way whenever investment in one sex becomes more profitable than investment in the other (Charnov, 1982). According to Bull (1983) this advantage is not available to pseudo-arrhenotokous species as a consequence of the diploid origin of both sexes. This is not a convincing argument, because the fact that it is the paternal chromosome which is eliminated also indicates that it is the mother who controls the chromosome elimination and possibly thereby also the sex of her offspring.

In this paper we will test the hypothesis that pseudo-arrhenotoky precludes sex-ratio control, by investigating phytoseiid mites known to have this particular genetic system (Schulten, 1985). These are mainly plant-inhabiting predators, well known for their successful use in controlling phytophagous mites in crops of economic importance (Helle and Sabelis, 1985). We will first review current knowledge on sex ratios of phytoseiid mites and then proceed by formulating a hypothesis on the relation between prey density and the mating structure of phytoseiid populations. Based on this hypothesis, a number of testable predictions are generated and validated using published and unpublished data. Finally, we will evaluate the consequences of our findings on sex ratio control in phytoseiid mites for our understanding of the selective advantages of pseudo-arrhenotoky.

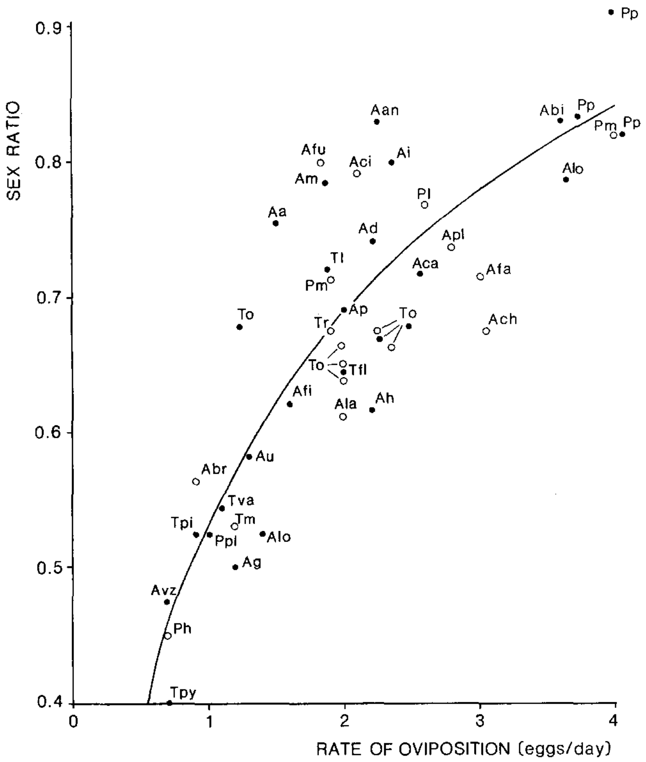
SEX RATIOS OF PHYTOSEIID MITES: A REVIEW

Most published data on sex ratios of phytoseiid mites originate from experiments where females were allowed to oviposit at high prey density, and their progeny was reared to adulthood to enable assessment of the sexes. In assembling the data set, the distinction was made between experiments where the broods were produced by single females isolated on a leaf disc (dark points, Fig. 1) and experiments that were not adequately described to tell whether the ovipositing females were single or in groups (open circles). Differential mortality between the sexes during development may hamper straightforward interpretation of the sex ratios among the mature offspring (e.g. Smith and Shaw, 1980), but juvenile mortality is generally very low, so that the use of these sex-ratio data is reasonable as a first approach to detect trends in data accumulated over the past 30 years.

As shown in Fig. 1, the proportion of daughters in broods of phytoseiid mites varies between 0.4 and 0.91. Most data indicate a female bias, and there are good reasons to believe that phytoseiid sex ratios vary between species (e.g. compare sex ratios of *Typhlodromus occidentalis* Nesbitt and *Phytoseiulus per-*

similis Athias-Henriot), between populations (e.g. Croft and McMurtry, 1972) and between strains (e.g. Hoy, 1984). Hoy (1985) suggested that the variability in sex ratios among different colonies and populations indicates a strong genetic component, but she also found variable sex ratios within colonies (Hoy, 1984) being the result of a small-sample bias or some hitherto unknown factors.

One way to understand this variability in sex ratios is to formulate and test hypotheses on adaptive sex-ratio responses to environmental conditions. Thus, the emphasis is not on *how* phytoseiids manage to produce female-biased sex ratios, but it is on the question *why* they do it. Answers to the latter question can be found only when it is recognized that natural selection favours individuals that maximize their contributions of genes to future generations (Charnov, 1982). This implies that a female can increase her fitness via two alternative pathways: gene tranfer via sons, or via daughters. Which of these alternatives is best (i.e. selected for) depends on the differential reproductive prospects of males and females, and hence on whether mating in phytoseiid populations is unlikely to be among relatives (i.e. random mating) or that there is a certain probability of brother-sister mating in these populations.



A HYPOTHESIS ON THE MATING STRUCTURE OF PHYTOSEIID POPULATIONS

Whether mating in a population of phytoseiid mites is random or not, largely depends on the extent of population mixing before mating (assuming absence of preferential sib-mating, for the sake of simplicity). Prey density is a major determinant of population mixing. Phytoseiid females invest a large amount of food in the production of an egg. Their eggs have a weight equivalent to 25% of their mother's weight. Thus, to acquire sufficient food to produce an egg, a phytoseiid female has to scan more and more leaf area with decreasing prey density. The distance between eggs of one particular female will therefore increase, and it becomes increasingly more likely that eggs of other females become interspersed. Although juvenile phytoseiids have low food requirements, there is a critical density (ca 1 prey per cm^2 infested leaf area) below which their tendency to disperse increases which further adds to population mixing before reaching the adult phase. Under these conditions, mating is likely to be random. For prey densities increasing above the critical threshold for juvenile

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Fig. 1. The relation between the mean oviposition rate and the sex ratio in the progeny of phytoseiid mites. Data of 34 phytoseiid species were selected from the literature and a few unpublished reports. They were all measured at ca. 25°C and ample supply of prey. The oviposition rate pertains to the mean number of eggs produced per day during the oviposition period. The sex ratio refers to the proportion of daughters in broods of single females on separate leaf-discs. Whenever the isolated state of the ovipositing females was uncertain (incomplete methods description), the sex ratios are indicated by open circles instead of dark points. The drawn line corresponds to the regression of the sex ratio (y) on the oviposition rate (x) after logarithmic transformation of x ($r = 0.844$): $y = 0.538 + 0.208\,x$. Abbreviated and complete scientific nomenclature of the phytoseiid species are given below together with references used to construct the figure: Aa, *Amblyseius andersoni* (Amano and Chant, 1978); Aan, *A. anonymus* (Dinh et al., 1988); Abi, *A. bibens* (Blommers, 1976); Abr, *A. brazilii* (El-Banhawy, 1975); Aca, *A. californicus* (Friese and Gilstrap, 1982); Aci, *A. citrifolius* (De Moraes and McMurtry, 1981); Ach, *A. chilenensis* (Ma and Laing, 1973); Ad, *A. degenerans* (Takafuji and Chant, 1976); Afa, *A. fallacis* (Ballard, 1954); Afi, *A. finlandicus* (M.W. Sabelis, unpublished data, 1982); Afu, *A. fustis* (Ezulike and Odebiyi, 1985); Ag, *A. gossypi* (Rasmy and El-Banhawy, 1975); Ah, *A. hibisci* (Tanigoshi et al., 1981); Ai, *A. idaeus* (Dinh et al., 1988); Ala, *A. largoensis* (Tanaka and Kashio, 1977); Alo, *A. longispinosus* (Shih and Shieh, 1979; Mallik and Channabasavanna, 1983); Am, *A. masiaka* (Blommers, 1974); Ap, *A. potentillae* (Sabelis, 1981); Apl, *A. pseudolongispinosus* (Xin et al., 1984); As, *A. scutalis* (Bounfour and McMurtry, 1987); Au, *A. umbraticus* (Knisley and Swift, 1971); Avz, *A. vazimba* (Blommers, 1974); Ph, *Phytoseius hawaiiensis* (Sanderson and McMurtry, 1984); Pl, *Phytoseiulus longipes* (Badii and McMurtry, 1984); Pm, *P. macropilis* (Prasad, 1967; Shih et al., 1979); Pp, *P. persimilis* (Takafuji and Chant, 1976; Friese and Gilstrap, 1982; M.W. Sabelis, C.J. Nagelkerke and K. Hofker, unpublished data, 1987; C.J. Nagelkerke (unpublished data, 1987, using a strain from Morocco)); Tfl, *Typhlodromus floridanus* (Tanigoshi and McMurtry, 1977); Tl, *T. longipilus* (Burrell and McCormick, 1964); Tm, *T. mcgegori* (Croft and Jorgensen, 1969); To, *T. occidentalis* (Tanigoshi et al., 1975; Friese and Gilstrap, 1982; Hoy, 1984; Sabelis, 1985); Tr, *T. rickeri* (McMurtry and Scriven, 1964); Tpi, *T. pini* (Charlet and McMurtry, 1977); Tpy, *T. pyri* (Overmeer, 1981); Tva *T. validus* (Charlet and McMurtry, 1977).

dispersal, population mixing is largely determined by the oviposition behaviour of the phytoseiid females. With increasing prey density, eggs of a particular female will tend to be deposited closer to each other, and it becomes less and less likely that eggs of other females will be deposited in between. The juveniles that develop from these brood groups stay near the place where they were born because their mother leaves sufficient food for their complete development. In addition, there is evidence that phytoseiid females avoid areas of a prey colony previously exploited by a conspecific female (Sabelis, 1981; Sabelis and Dicke, 1985). These areas are probably detected by a marking pheromone left by the first visitor, maybe also by physical contact with her (or her eggs), and certainly also by the decreased availability of prey (though sufficient to the juveniles, insufficient for the high food requirements of egg-producing females) as a consequence of predation by the first visitor. In this way, phytoseiid females foraging in a colony of spider mites tend to space out over the available food source and give rise to more-or-less distinct groups of eggs and juveniles that, when mature, first start mating and then disperse to other – preferably unexploited – prey colonies. There is evidence that the first mating is decisive for the fertilization of most if not all eggs produced by a female. (It is interesting to note that the minimum number of matings required to realize full fecundity is one in the more fecund phytoseiid species, whereas two matings are needed in the species with lower fecundities; how many matings per female succeed the first one is not known, however, but their success in sperm transfer is probably low). The consequence of all this is that the probability of sib-mating increases with prey density. Future research should give more definite proof of the relation between prey density and the probability of sib-mating. However, for the time being, this hypothetical relationship seems a reasonable starting point.

Prey density is not a very practical measure, because some well-investigated phytoseiids are known to differ in the composition of their diet (Sabelis and Dicke, 1985), and the diet of most phytoseiids is not known. Sabelis (1985) argued that the mean oviposition rate (measured at high prey density and a standard temperature of ca. 25°C) is a more useful measure because plenty of data are available from the literature, and because one may expect a relation between the mean oviposition rate and the characteristic density of its preferred prey species. At one extreme, phytoseiids with high oviposition rates are usually specialized on high-density prey types. For example, *P. persimilis* females produce ca. 4 eggs per day at 25°C, and prefer spider mites of the genus *Tetranychus* that usually attain local densities of ca. 40 prey per cm^2 colonized leaf area. At the other extreme, phytoseiids with low oviposition rates prefer low-density prey types. For example, females of *Amblyseius potentillae* (Garman) produce ca. 2 eggs per day at 25°C, and prefer spider mites in the genus *Panonychus* that usually attain local densities of 2–4 prey per cm^2 colonized leaf area. These large differences in local densities characteristic to the preferred prey species are likely to have important consequences for the selection pressure on the rate of egg production, because egg production requires much food. For this reason, it is expected that selection for speeding-up the conversion of food into egg biomass is less intense for phytoseiids preferring low-density prey types than it is for phytoseiids preferring high-density prey types. Indeed, as discussed by Sabelis (1985), available evidence suggests a relation between the mean oviposition rates characteristic to a phytoseiid species, and the density characteristic to its preferred prey species (measured in absence of predators). Thus, it may be concluded that oviposition rates characteristic to a phytoseiid species may depend on the characteristic density of its preferred prey species, and that oviposition rates are therefore positively related to the probability of brother-sister mating among the broods of the phytoseiid predator. The higher the prey density, the higher the oviposition rate of the predator and the probability of sib-mating among its progeny. Of course, this hypothetical relationship needs further testing, but it seems a reasonable first step in trying to make sense out of the variability in sex ratios among phytoseiid species, as will be shown below.

NATURAL SELECTION AND THE SEX RATIO UNDER RANDOM MATING

It is possible to theorize on sex-ratio evolution without particular reference to a sex-determining mechanism. Fisher (1930) proposed that sex ratio could evolve as a product of selection maximizing the contribution of the individual's genes to future generations. Assuming that (1) the population is infinitely large, (2) the costs (in terms of maternal resources) of producing a son or a daughter are equal, and (3) the sex ratio does not interact with these costs or with the survival and the quality of the offspring, he argued that in a population where males are rare, a female who produces an excess of sons would have an above-average genetic input to the next generation (and vice versa if daughters are rare). Hence, if the primary sex ratio in the population is 0.5, a mother cannot increase her relative contribution of genes by altering the sex ratio of her offspring from 0.5. Because no other sex ratio can do better, a sex ratio of 0.5 is called an 'evolutionarily stable sex ratio' (Maynard Smith, 1978). This is essentially a population's primary sex ratio, which does not require that different females make the same allocation to sons and daughters, but only that the population balance is half daughters, half sons. This seems to contrast with the constant individual sex ratios usually found among the progeny of one individual. However, for a finite population the evolutionarily stable tertiary sex ratio tends to reduce to an individual's strategy because, on average, individuals producing half sons, half daughters, are favoured (Taylor and Sauer, 1980). A sex ratio of 0.5 is therefore to be expected in broods of each phytoseiid female. Perhaps this hypothesis needs a slight modification, because Fisher

TABLE 1

Influence of prey availability total fecundity, oviposition rate and sex ratio of three phytoseiid species at 26° ± 2.6°C (data from Friese and Gilstrap, 1982)

Phytoseiid species	No. prey eggs provided daily	Total fecundity (eggs ♀$^{-1}$)	Oviposition rate (eggs ♀$^{-1}$ day^{-1})	Proportion daughters	No. ♀ tested
P. persimilis	40	76.5	3.8	0.83	12
	10	49.9	1.8	0.59	15
	5	17.5	0.9	0.47	15
	3	2.1	0.5	0.33[a]	15
T. occidentalis	40	9.4	1.2	0.68	11
	10	11.7	1.1	0.58	15
	5	11.1	1.2	0.71	15
	3	8.0	0.6	0.43	15
A. californicus	40	41.0	2.6	0.70	9
	10	35.6	2.1	0.66	15
	5	31.7	1.3	0.56	15
	3	17.5	0.8	0.52	15
	1	7.3	0.5	0.43	15

[a] Note that this low value might be the consequence of a small sample bias since total fecundity is very low.

(1930) predicted equal investment in both sexes in terms of maternal resources and the costs of producing a son or a daughter are unlikely to be exactly the same. For example, if egg weight reflects maternal investment, sons are cheaper than daughters. C.J. Nagelkerke, K. Hofker and M.W. Sabelis (unpublished data, 1987) found that the son-daughter ratio of egg weights of *P. persimilis* is 1:1.15 so that the evolutionarily stable proportion of daughters is 0.465 rather than 0.5.

Random mating is a reasonable assumption for (1) phytoseiid species that have a diet consisting of low-density prey types and (2) for phytoseiid species that are specialized on high-density prey types, but currently experience low prey densities. Under both these conditions, oviposition rates are low and sex ratios are expected to tend toward 0.5. These predictions can be validated using data from the literature. Figure 1 provides evidence for the first prediction; sex ratios approximate 0.5 when oviposition rates are low. For example, *Typhlodromus pini* (Chant) and *T. validus* (Chant) produce only 1 egg per day when food is abundant and peak densities of *Oligonychus* mites, their main prey in California pine trees, correspond to 1 mite per 12 needles. These two phytoseiid species produce secondary sex ratios of 0.53 and 0.54 respectively (Charlet and McMurtry, 1977). Similarly, a sex ratio of ca. 0.5 has been found in the offspring of females of *Typhlodromus pyri* Scheuten and *Amblyseius vazimba*

Blommers and Chazeau, which produce only 0.7 eggs per day under favourable conditions and cannot exploit high-density prey types, such as two-spotted spider mites, because they are hindered by the complex web produced by this prey (Blommers, 1974; Overmeer, 1981). All these examples are in agreement with the prediction for phytoseiids with a diet consisting of low-density prey types. There also exists evidence of equal investment in the sexes for phytoseiids with a diet of high-density prey types when current prey density is low. Veltkamp (1968) and Friese and Gilstrap (1982) collected eggs deposited by phytoseiids at various prey densities and reared them to adulthood at high prey density for determination of sex. The sex ratios measured in this way appeared to be female-biased at high prey density, but they approached unity at the lowest prey densities, where random mating is expected to be the rule (Table 1). These experiments strongly suggest that phytoseiid mites are capable of sex-ratio control. Even more interestingly, the experiments were done precisely with the phytoseiid species where the diploid origin of the males and paternal genome loss are proven facts: *P. persimilis* and *T. occidentalis* (Helle et al., 1978; Hoy, 1979; Nelson-Rees et al., 1980; Schulten, 1985). Why then are the sex ratios of most phytoseiid species so heavily skewed towards females? Bull (1983) showed that a female bias is possible under random mating, in systems where male haploidy arises from paternal genome loss and where sex determination is a property of the zygote's genotype irrespective of which parent contributes the sex factors. His model cannot account for sex ratios more extreme than 0.66, but it may contribute to the female bias observed in the broods of many phytoseiid species. Bull (personal communication, 1986) pointed out that mother-offspring conflict over the sex ratio could yield any sex ratio between 0.5 and 0.66 because different populations have different genetic histories and the outcome of mother-offspring conflict is very sensitive to the genetics of sex determination.

NATURAL SELECTION AND THE SEX RATIO UNDER SIB-MATING

Female-biased sex ratios can be the result of selection processes operating in spatially structured populations (Hamilton, 1967; Maynard Smith, 1978; Colwell, 1981; Wilson and Colwell, 1981; Charnov, 1982). Frank (1985, 1986) showed that there are at least three truly causal mechanisms: (1) inbreeding within local groups; (2) local mate competition between related males; and (3) genetic differentiation among groups (and genetic correlation within groups). Populations of most phytoseiid species typically have a demic structure, especially because phytophagous spider mites, their most important prey, have a strong tendency to form patchy infestations. Within these patches, phytoseiid females deposit their eggs and mixing of their local populations before mating depends on the distribution of the eggs by the females and on the mobility of the juveniles and unmated matures. As argued before, high local prey

TABLE 2

Mean oviposition rates and the proportion of daughters among the lifetime offspring of *T. occidentalis* at two densities of conspecific predators and under conditions of abundant prey eggs (*Tetranychus urticae* Koch)

No. predators per leaf-disc ($5\ cm^2$)	No. prey eggs provided daily	Oviposition rate (eggs ♀$^{-1}$ day^{-1})	Proportion diploid eggs	No. eggs 'sexed'	No. ♀'s tested[a]
1	50	2.3	0.67	311	8
10	200[b]	1.3	0.54	1271	5×10=50

The sex ratio was determined from chromosome counts in egg squashes treated with orceine. In this way 1-day-old eggs of the predators were sexed with more than 97% success (Data from Mentink, 1982). Environmental conditions: 26°C, 70% r.h. and continuous light.

[a] Predator females that escaped from the leaf disc were replaced by females from an extra series of parallel experiments under exactly the same conditions of prey and predator density.

[b] Note that it would have been more logical if Mentink had supplied 500 prey eggs instead of 200 eggs daily. However, realizing that a *T. occidentalis* female consumes 10 prey eggs per day when foraging alone at a prey density of 50 eggs, then it follows that the actual prey density during a day may vary maximally between 200 and 100 eggs per leaf-disc. Hence each of the 10 predators 'experiences' prey-egg densities during each day that are even higher than the single predator female 'experiences' at the prey density of 50 (to 40) eggs.

TABLE 3

Mean proportion of daughters in offspring of single *P. persimilis* females in absence or presence of cues (eggs, faeces or marking pheromones) left by three conspecific during the day preceding the 3-day experiment

Cues	Proportion daughters			Eggs ♀$^{-1}$ day^{-1} (mean)	No. ♀'s
	day 1	day 2	day 3		
–	0.73	0.84	0.83	4.3	37
+	0.67	0.71	0.72	3.5	46

Eggs were collected each day and reared to adulthood for sex determination (with more than 91% success). From M.W. Sabelis, C.J. Nagelkerke and K. Hofker (unpublished data, 1987)

density causes the broods of each female to become clumped and causes low mobility of juveniles and unmated matures. Hence, the probability of sib-mating is expected to increase with prey density.

These considerations lead to two testable predictions: (1) phytoseiid species that are specialized on high-density prey types are capable of producing female-biased sex ratios when prey density is high; but (2) these species tend to produce half sons, half daughters when predator density is high, even when prey is abundant. The first prediction is supported by the results of Friese and

TABLE 4

Mean proportion of daughters in relation to the total number of eggs produced per female in the 3-day experiment (See Table 3 and text for experimental set-up)

Cues	Number of eggs per female per 3 days								
	3-4	5-8	9	10	11	12	13	14	15
–	0.50 (1)	-	0.78 (1)	0.78 (5)	0.77 (4)	0.80 (6)	0.78 (9)	0.82 (7)	0.85 (4)
+	0.70 (10)	0.76 (10)	0.58 (3)	0.70 (4)	0.71 (7)	0.72 (8)	0.58 (3)	0.75 (1)	-

Numbers of females in each fecundity class are given in brackets. From M.W. Sabelis, C.J. Nagelkerke and K. Hofker (unpublished data, 1987).

Gilstrap (1982, and Table 1). Females of three phytoseiid species appear to produce female-biased sex ratios when prey density is high, whereas they produce a sex ratio of ca 0.5 when prey density is low. These results, together with the data presented in Fig. 1, show that specialists of high-density prey types have higher oviposition rates and produce the more extreme female-biased sex ratios. For example, *P. persimilis* is a predator that feeds preferentially on densely packed aggregations of spider mites in the genus *Tetranychus*. The densities of these prey mites amount to ca. 40 mites per cm^2 colonized (webbed) leaf area. The rate of oviposition of *P. persimilis* females is among the highest known of any phytoseiid, and it is the sex ratio of this very species that is extremely female-biased; the proportion of daughters in the progeny varies between 0.8 and 0.91. The same agreement is found in the other specialist predators of *Tetranychus* mites, such as *Phytoseiulus macropilis* (Banks), *Phytoseiulus longipes* Evans and *Amblyseius bibens* Blommers. Other phytoseiid species, such as *Typhlodromus caudiglans* Schuster, *Amblyseius fallacis* (Garman) and *T. occidentalis* are specialized on *Tetranychus* mites, but can rely on low-density prey types, such as *Panonychus* mites. These have somewhat lower rates of oviposition and their sex ratios lie between 0.66 and 0.84. Another category of phytoseiids, among which are *Amblyseius potentillae* and *A. finlandicus* (Oudemans) consists of predators that are hindered by the webs of *Tetranychus* mites, but forage successfully for *Panonychus* mites which do not make complex webs. These phytoseiid species generally show lower rates of oviposition and sex ratios of ca. 0.66 or lower. However, some of the observed variation in Fig. 1 remains unexplained. Rather than attempting to explain all this it seems more constructive to formulate more detailed hypotheses and set up experiments for testing. For example, it would be interesting to compare sex ratios of phytoseiid species with similar diets but differences in the probability of successful sperm transfer during second and subsequent matings. It is expected that sex ratios will tend to be less female-biased when sperm transfer during second and later matings tend to be more successful. This is because population mixing before the second and later matings will be more intense due to the high food requirements of the predator females and the concomitant high tendency to disperse to more profitable prey areas.

The second prediction mentioned above is based on a model by Werren (1980) and tested for the case of parasitic wasps (Werren, 1983; Waage and Lane, 1984; Waage and Sook Ming, 1984). It was found that, as the number of foundresses contributing to a local mating population increases, the sex ratio among the progeny shifts from a female bias towards 0.5. Recently, very similar trends were found in sex-ratio data from experiments with phytoseiid mites where predator density was varied and prey density was maintained at a high level. Mentink (1982; as cited in Sabelis, 1985) was the first to show a decrease of the proportion females with increasing density of the predator *T. occidentalis* (Table 2). Using the same predator, very similar results were obtained by M.W. Sabelis, C.J. Nagelkerke and K. Hofker (unpublished data, 1987). They found a sex ratio of 0.68 for single females, whereas a sex ratio of 0.52 was found when 10 predator females together foraged and oviposited on the same leaf disc. Stimulated by these results, Dinh et al. (1988) assessed the effect of crowding of female predators on progeny sex ratios using different phytoseiid species: *Amblyseius idaeus* Denmark and Muma and *A. anonymus* Chant and Baker. They also found that the female bias in the sex ratio vanished under conditions of predator crowding (20–30 females per 25-cm^2 bean leaf). The most conclusive evidence of an effect of predator density on sex ratio was obtained by M.W. Sabelis, C.J. Nagelkerke and K. Hofker (unpublished data, 1987). They investigated the effect of cues left on a leaf disc by conspecific predators (the first visitors) on the sex ratio in the brood of a single female (the second visitor) placed on the same leaf disc after removing the first visitors. This experimental set-up allowed unambiguous assessment of sex-ratio changes in the broods of single females at high prey density and with cues of first visitors absent or present. The results of experiments with *P. persimilis* are presented in Tables 3 and 4. Table 3 shows that a sex-ratio shift due to the presence of first visitor's cues becomes manifest on the second and third day of oviposition by the second visitor. In addition, Table 4 shows that this sex-ratio shift occurs within all classes of females producing equal brood sizes (except for the lowest brood-size class). This is strong evidence that sex ratio shifts do not occur as a result of a simple son-first pattern in combination with an effect of predator cues on brood size, but that it is the result of genuine sex-ratio control. It should also be noted that this evidence was obtained for phytoseiid species whose pseudo-arrhenotokous state is well documented by cytological and or genetical evidence (Helle et al., 1978; Hoy, 1979; Nelson-Rees et al., 1980).

DISCUSSION

This review of current knowledge on sex ratios in the Phytoseiidae shows ample evidence of sex-ratio control under pseudo-arrhenotoky. This is a fascinating result which should challenge physiologists and geneticists to investigate how maternal control is achieved. Such a control mechanism requires an appropriate sex-determining mechanism. Paternal genome loss might be conditional upon sex factors determining maleness, but there is no evidence that this is the case. It may just as well be true that maleness is conditional upon paternal chromosome loss. In any case, paternal chromosome loss requires both the ability to discriminate between paternally and maternally derived chromosomes and the ability to inactivate and eliminate exclusively the paternal chromosome set. To what extent chromosomal or extrachromosomal factors such as parasites play a role in determining the sex (ratio) remains to be investigated.

It is interesting to note that the proportion of daughters in a brood is usually positively related to the oviposition rate. This is exemplified by the decrease in sex ratio and oviposition rate (1) in the data presented in Fig. 1; (2) with decreasing prey density (Table 1; Veltkamp, 1968; Friese and Gilstrap, 1982); (3) with increasing predator density (see Tables 2 and 3); (4) with temperatures decreasing below 20°C (e.g. *Amblyseius chilenensis* Dosse (Ma and Laing, 1973); *T. occidentalis* (Tanigoshi et al., 1975; Wiegers, 1981), and *A. hibisci* Chant (Tanigoshi et al., 1981)); and (5) just after food deprivation of the predator female, in *P. persimilis* (Amano and Chant, 1978). This relation is probably not causal because the results in Table 4 show that the effect on the sex ratio is independent of brood size (and thus also independent of the oviposition rate). It is more likely that, though independent, the effect on the sex ratio and the effect on the *mean* oviposition rate are often, if not always, in the same direction. Why these two effects happen to concur under various circumstances, is not always clear. For example, it may be questioned what the adaptive value is of lower sex ratios at low temperatures and why female predators produce eggs at a lower rate at high predator densities even when prey density is high (or, rather, kept high by the experimenter).

To return to the questions on adaptive significance of pseudo-arrhenotoky (see Introduction), some answers are obtained. Clearly, Bull's (1983) suggestion, that sex-ratio control may constitute one advantage for the evolution of arrhenotoky relative to pseudo-arrhenotoky, needs revision. Perhaps a better reason for arrhenotoky to be selectively superior to pseudo-arrhenotoky is its advantages at low densities, when it may become difficult for the female to obtain mates. Would this be a reason why psuedo-arrhenotoky in phytoseiid mites is likely to be an unstable intermediate state between diploidy and arrhenotoky ? With respect to phytoseiid mites we are inclined to think that the answer is no. Sabelis and Van der Meer (1986) carried out several population experiments with the predatory mite *P. persimilis*; the predators were released in a patch with numerous prey mites, and the subsequent measurements of population numbers and dispersal show that dispersal occurs by mated females, and that it tends not to occur until after a period of rapid population build-up ended by the virtually complete elimination of the prey. Thus, just before the period of dispersal the predators are very numerous and all gathered together within the host-plant area colonized by their prey. Hence, it is unlikely that females fail to find a mate. Moreover, the dispersal tendency is very low in juveniles, males, and uninseminated females. The dispersers are predominantly (if not exclusively) the inseminated adult females. Thus, as long as phytoseiid mites experience high probabilities of obtaining mates, parthenogenetic production of sons will be of little use as a way to guarantee sperm supply. Selection for arrhenotoky will thus be weak unless other factors cause sudden crashes of phytoseiid populations. Such crashes do occur in populations of the phytophagous prey mites such as spider mites. Local extermination of spider mites by phytoseiid mites seems to be a frequent phenomenon. Most interestingly, spider mites are arrhenotokous. Thus, if a diploid egg or juvenile spider mite happens to escape from predation, these individuals would greatly profit in that, when mature, they can be inseminated by their own sons. This is a very relevant observation with respect to the consequences of the use of pesticides in agricultural practice. Clearly, spider mites, being arrhenotokous, profit from their ability to produce sons when the individual surviving a pesticide application happens to be a virgin female, whereas a surviving pseudo-arrhenotokous mite cannot produce any offspring when virgin. Pesticide application may thus pose very serious problems for phytoseiid mites with an evolutionary history without frequent population crashes, but less so for spider mites with an evolutionary history characterized by frequent population crashes (e.g. due to phytoseiid mites, epidemics of fungi etc; crashes of phytoseiid populations due to their natural enemies and pathogens have not been reported in the literature).

In conclusion we hypothesize that the maintenance of pseudo-arrhenotoky depends on ecological conditions determining a sufficiently high probability of mate finding. It would be interesting to test this hypothesis for other pseudo-arrhenotokous arthropods such as some oribatid mites, and sciarid and scale insects, and to assess whether arrhenotoky tends to occur under conditions where the probability of mate-finding is frequently low.

When pseudo-arrhenotoky and arrhenotoky are equivalent in sharing the two-fold advantage to the mother and in providing possibilities for sex-ratio control, and if pseudo-arrhenotoky occurs whenever the probability of mate finding is high, whereas arrhenotoky occurs whenever this probability is low, we have a strong indication that there must be an advantage to pseudo-arrhenotokous individuals in retaining the diploid state during at least the early cleavage phases of embryonic development. In our view, the detection of this advantage is crucial to our understanding of the evolution of pseudo-arrhenotoky. We suggest that there is a possible advantage to retention of the diploid state accruing from repair of the maternal genome via copies of the equivalent part of the paternal genome. Errors in the maternal genome might be fatal to the very early stages of embryonic development. The paternal genome is unlikely to contain the same errors and may, therefore, be suitable to reinstal lost genetic information. After several mitotic divisions, however, the risk of fatal errors is spread over all cells in the embryonic tissue so that the paternal chromosome is of little use as a template for DNA-repair and may therefore be inactivated and eliminated. Elimination may be advantageous to reduce the DNA-load and to re-allocate scarce nutrients. Cavalier-Smith (1978) suggested that the smaller inventory of DNA may in turn imply a faster mitotic cycle-time. A higher rate of development of the males is not only a fact, but it is also selectively advantageous to the males in maximizing the number of matings obtained. Despite these advantages of the haploid state the male starts as a diploid which suggests an advantage, such as DNA-repair using the paternal chromosome as a template. It is worthwhile to note that there might be a role of paternal chromosomes in sex differentiation and male fertility, as shown for many pseudo-arrhenotokous organisms (Nelson-Rees, 1962; Brown and Nur, 1964). Hence, retention of the initial diploid state may be advantageous unless there is a substantial risk to the females of becoming a wall-flower, a situation where parthenogenetic production of sons is clearly the more suitable genetic system.

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